

THE ONTOGENY OF SWIMMING BEHAVIOR IN THE  
SCYPHOZOAN, *AURELIA AURITA*. I. ELECTRO-  
PHYSIOLOGICAL ANALYSIS <sup>1</sup>

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The life cycle of a scyphozoan coelenterate typically includes several developmental stages with strikingly different morphologies and distinct behavioral repertoires. The large, motile medusae produce gametes which, upon fertilization, develop into planulae larvae. Planulae settle on a substrate and grow into sessile polyps termed scyphistomae. Scyphistomae feed and produce other scyphistomae by budding. Seasonally the scyphistomae produce new medusae by transverse fission. A series of grooves forms perpendicular to the oral-aboral axis and the segments formed metamorphose into larval medusae called ephyrae. Development of ephyrae proceeds in an oral-aboral direction on the polyp, the most oral segment is the most advanced and is the first to be released as a free ephyra. This process of medusa production is termed strobilation, and the transversely segmented polyp is called a strobila. The aboral portion of the strobila, where segmentation has not occurred, develops tentacles. When all the ephyral segments have been released the remaining polyp feeds and repeats the strobilation process the following season. The released ephyrae develop into large, sexual medusae, completing the life cycle.

Behavior of scyphozoans has been most extensively studied in the adult medusae, with particular attention having been given to the control of the rhythmic swimming pulsations. These pulsations are initiated by marginal ganglia (rhopalia) located in the periphery of the bell (Romanes, 1876). Spontaneous discharges from pacemakers of the rhopalia spread through a rapidly-conducting nerve net (giant fiber nerve net, GFNN) located in the subumbrellar ectoderm. GFNN activity evokes contractions of the swimming muscles and coordinates the swimming beat (Romanes, 1876; Schäfer, 1879; Horridge, 1953, 1954, 1956a). The swimming muscles of medusae are striated with the characteristic birefringent and nonbirefringent pattern seen in the muscles of more advanced animals. There is also a diffuse, more slowly-conducting nerve net (diffuse nerve net, DNN), which modulates pacemaker activity through polarized synapses and also serves to control marginal tentacle activity (Romanes, 1877; Horridge, 1956a, 1959; Passano, 1965).

The behavior of a newly-released ephyra differs somewhat from that of adult medusae. The released ephyra exhibits three behavioral responses of importance: first, rhythmic swimming involves the simultaneous folding of the eight arms toward the mouth; secondly, feeding involves the coordinated movement of the

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manubrium and an individual arm; and thirdly, spasm, which occurs during strong stimulation, involves all the arms as in swimming, but the contraction is tonic and can last several minutes (Horridge, 1956a). Physiological analysis of these three responses in company with histological examination has demonstrated the presence of two conducting systems controlling ephyral behavior. The GFNN propagates the swimming beat while the DNN is responsible for feeding and spasm (Horridge, 1956a). The ephyral responses, feeding and spasm, are not observed in adult medusae, although both medusae and ephyrae possess diffuse and giant fiber nerve nets.

Chapman (1965, 1966) has described the behavior of scyphozoan polyps and the organization of the musculature associated with that behavior. Scyphistomae of *Aurelia aurita* have no striated muscles, show no spontaneous activity, and respond only sluggishly to mechanical stimulation. Prey is captured by nematocysts on the tentacles and transferred to the mouth by tentacular bending. Contact between the mouth and tentacles during feeding is followed by mouth opening. Chapman proposes that the responses of the polyp are coordinated mechanically rather than neurally. In this view a localized response in one part of the animal mechanically stimulates and causes a response in another part of the animal. There is a nerve net in *A. aurita* polyps, but neither sensory nor pacemaker cells have been morphologically identified (Chapman, 1965). Although electrophysiological techniques have been used successfully in other coelenterate polyps (*e.g.*, Josephson, 1965; Josephson and Macklin, 1969; McFarlane, 1969; Morin and Cooke, 1971; Rushforth, 1971; Ball, 1973; Ball and Case, 1973; Spencer, 1974a; Stokes, 1974; early work summarized in Bullock & Horridge, 1965), these have not previously been used with scyphozoan polyps.

During strobilation, polyp behavior becomes transformed into that of the medusa. The ephyrae attached to a strobila begin beating well before their release, and each beats independently of its neighbors. Autonomy of behavior in a strobila is not complete however, since the entire strobila will shorten when stimulated (Horridge, 1956a).

The transformation of a sessile, phlegmatic polyp to an active, swimming medusa is dramatic. During the transformation the polyp develops clear neurological control mechanisms; most obvious are the spontaneously active pacemakers interconnected by a fast, through-conducting nerve net. Thus at the oral end of the strobila are beating ephyrae with pacemakers and giant fiber nerve nets coordinating the striated swimming muscles, while at the aboral end of the strobila is a tentaculate polyp lacking spontaneous activity, obvious neurological coordination, or striated muscles. The strobila, then, is a chimera of the morphology and behavior of both polyp and medusa presented in a developmental gradient along the oral-aboral axis. The purpose of this investigation is to take advantage of the developmental gradient expressed by the strobila and investigate the ontogeny of swimming behavior in a scyphozoan medusa. Particular attention is given to the tentacular behavior of the polyp, since the tentacles of the polyp are developmentally homologous with the rhopalia of medusae (Thiel, 1966), and it is the rhopalia which initiate the swimming beats in medusae. This paper describes the electrophysiological changes which occur during the metamorphosis of the polyp into a strobila. A second paper will consider the physiological changes which occur during the

transformation of the polyp to medusa by describing the differential responses of the different stages of the life cycle to ions and drugs.

#### MATERIALS AND METHODS

##### *Medusa*

Medusae of *Aurelia aurita* (5–8 cm in diameter) were collected from the Eel Pond, Woods Hole, Massachusetts. Collected medusae were kept in a deep tank with slowly flowing sea water until they were used.

Suction electrodes were used to record the spontaneous pacemaker potentials in the marginal ganglia. Fine electrode tips were made by pulling 1 mm glass capillary tubing on a standard micro-electrode puller, breaking the tips, grinding them flat on a dry Arkansas oil stone, and fire polishing the tips with a micro-burner to a 50  $\mu$ m opening. This procedure produced smooth, flat electrode tips which minimized tissue damage and provided a tight seal.

Marginal ganglion activity and the associated mechanical swimming contractions were recorded simultaneously from a 45° segment of a medusa. The tissue wedge was excised by cutting along the adradii adjacent to a marginal ganglion and pinned aboral-side up in a constant-temperature chamber maintained at the same temperature as the animal holding tank (15–18° C). A hook placed through the mesoglea at the apex of the wedge was attached to a force-displacement transducer to record contractions. Potentials from marginal ganglia were recorded with a glass suction electrode attached to the aboral surface of the rhopalium near the ocellus. Potentials were recorded between the suction electrode and an indifferent, Ag/AgCl bath electrode. Recorded activity was amplified by a high gain AC-amplifier with a long-time constant. Both mechanical and electrical events were displayed on a penwriter. Marginal ganglion potentials from isolated ganglia were recorded in a similar manner.

##### *Scyphistoma*

Scyphistomae of *A. aurita* were obtained from the Supply Department of the Marine Biological Laboratory, Woods Hole, Massachusetts, and also raised from planulae released from medusae of *A. aurita* collected from the Eel Pond. Some additional polyps (Woods Hole strain) were obtained from Dr. Dorothy Spangenberg (University of Colorado, Boulder, Colorado).

Strobilation of scyphistomae usually occurs in the presence of I<sup>-</sup>. To prevent strobilation, the scyphistomae were maintained in I<sup>-</sup>-free artificial sea water (ASW). Individual polyps were isolated in, and allowed to attach to, 13 × 9 mm test containers which were placed in storage dishes containing 250 ml I<sup>-</sup>-free ASW prepared by passing ASW (463.0 mM Na<sup>+</sup>, 9.9 mM Ca<sup>+2</sup>, 9.7 mM K<sup>+</sup>, 51.2 mM Mg<sup>+2</sup>, 538.6 mM Cl<sup>-</sup>, 27.0 mM SO<sub>4</sub><sup>-2</sup>, and 2.3 mM HCO<sub>3</sub><sup>-</sup>) through an ion exchange resin (AG1-X2, BioRad Laboratories; see Spangenberg, 1971). The test containers with the isolated polyps could be removed from the storage dishes either for exchanging the culture medium or experimental purposes without disturbing the polyps. All polyps were kept at 4° C and fed twice weekly with newly hatched *Artemia salina* nauplii. Several hours after feeding the culture, the medium was replaced with fresh I<sup>-</sup>-free ASW to remove uningested nauplii.

Polyps were electrically stimulated by platinum pin electrodes, 75  $\mu\text{m}$  in diameter, insulated to the tip with teflon, and mechanically stimulated with a hair attached to a glass rod. Suction electrodes, similar to that used with medusae, were used to record electrical activity.

Tentacle activity was detected by a fiber optics probe which monitored movement without contact with the animal. The probe was constructed by passing a 50 cm long  $\times$  200  $\mu\text{m}$  fiber optics light guide down the bore of an L-shaped, 1 mm O.D. glass capillary tube so that one end of the light guide protruded 1 mm from the short end of the "L". Two similarly prepared light guides were attached to a glass rod so that the short ends of the "L"s were pointing at each other. Light from a microscope illuminator was passed down one light guide, and the free end of the second guide was inserted into a light tight box containing a selenium photo-voltaic cell. The tips of the light guides were 1 mm apart and aligned for maximum output, then placed over a polyp so that a tentacle came between the tips of the probe. Since the tentacle is translucent, any slight movement altered the amount of light reaching the photocell. The shape and amplitude of the photocell output were not necessarily linearly related to tentacle movement, but the output of the photocell gave an accurate representation of the onset of movement. The output of the photocell was amplified and displayed on one channel of an oscilloscope or penwriter, while the potentials recorded from the same tentacle as the mechanical events were displayed on another recording channel.

The fiber optics probe could not be situated to detect lip movements. Lip behavior in the immediate area of the suction electrode was monitored visually and was recorded along with the electrical events by manually triggering an event marker on the penwriter.

### *Strobila*

Polyps of *A. aurita* attached to individual test containers and cultured in I-free ASW, as described previously, were induced to strobilate by replacing the I-free ASW with  $10^{-5}$  M KI in ASW and continuing all other procedures (Spangenberg, personal communication). Strobilation occurred in 6–8 weeks in all cultures so treated.

The mechanical and electrical recording methods used on the scyphistoma were also used on the strobila. Experiments on both scyphistoma and strobila stages were carried out in a constant temperature chamber maintained at 4° C.

## RESULTS

### *Medusa*

As has been previously reported (Horridge, 1953, 1954), in medusae there is a one-to-one correspondence between the potentials recorded from a marginal ganglion and swimming contractions (Fig. 1A). A contraction of the swimming muscles follows a marginal ganglion potential (MGP) after a latency of approximately 300 msec. MGPs from isolated ganglia are produced at regular intervals for extended periods of time (Fig. 1B).



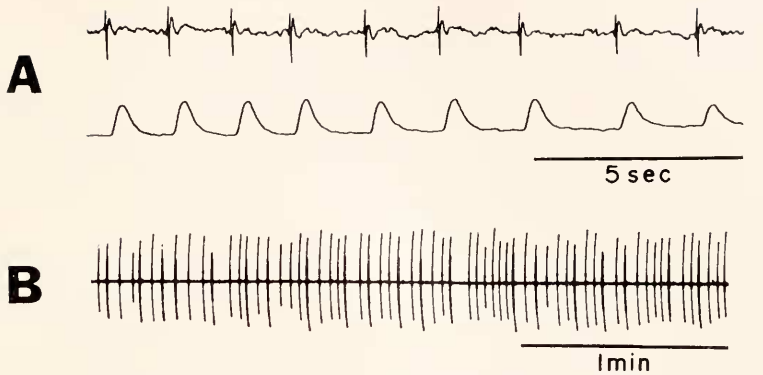


FIGURE 1. Electrical activity and behavior of adult medusae. A, portion of a record from a 45° segment of a medusa; the upper trace shows marginal ganglion potentials (MGPs), the lower trace is a simultaneous recording of mechanical activity. B, MGPs from an isolated marginal ganglion. Voltage calibration is 20 mV.

### *Scyphistoma*

Several types of spontaneous polyp movements were observed in the absence of any apparent stimulation. During an extended observation period most of the tentacles can be seen to contract at one time or another in no set pattern. Each tentacle, when it contracts, shortens without bending and, after a time, slowly elongates. Sometimes the tentacle shortening is the result of a series of small contractions, the whole process occurring in one or two seconds. A single contraction of a restricted, localized portion of a tentacle may occur, resulting in either a shortening, a bending, or at times, the forming of a loop. Bending of an individual tentacle on the oral side brought the tentacle toward the mouth or completely into the mouth and is typical of the feeding response. If the tentacle was inserted into the mouth, a short time later the tentacle would be retracted from the coelenteron with bending occurring at the base of the tentacle followed by the relaxation of the muscles on the oral side. This tentacle behavior was the only one which was associated with mouth behavior. Infrequently a tentacle, in the normal extended position, bent aborally by contracting aboral muscles at the base of the tentacle. Rarely, the tentacles were bent completely parallel to the column. Occasionally all of the tentacles contracted simultaneously. In this behavior the tentacles also bent simultaneously at the bases causing the tentacle tips to meet at the oral-aboral axis above the mouth forming an arch over the oral disk.

Two types of spontaneous lip behavior were seen, localized retraction and flaring. During a flare the entire lip retracts causing the mouth to gape. Both lip behaviors can occur in the absence of tentacular activity; however, lip flaring also occurs as a tentacle bends toward the mouth during feeding as mentioned above.

Spontaneous activity of the column is infrequent. The column can shorten either symmetrically or asymmetrically. Complete symmetrical shortening of the column results from a series of short symmetrical contractions. Symmetrical contractions of the column were always accompanied by the simultaneous shortening and folding of the tentacles over the mouth. This behavior is probably a protective response.

The synchrony of tentacles and column contractions in this response indicates that the protective response is coordinated.

Electrical stimulation of the tentacles caused only the contraction of the individual tentacle stimulated. Similarly, the only effect resulting from electrical stimulation of the lip was a localized retraction of the lip in the area stimulated. Symmetrical column shortening could be initiated by stimulating any portion of the animal but required stimuli considerably stronger than that used to initiate tentacle contractions.

Gentle mechanical stimulation with a hair usually did not elicit a response from either the lip or tentacles. In those cases where a response occurred, the tip would retract locally, or the stimulated tentacle would shorten and occasionally bend toward the mouth and insert into the coelenteron. Once, when a tentacle was touched on the external side, it responded with a localized contraction and bent aborally. Vigorous mechanical prodding of the column never caused a response; however, such stimuli on the tentacles often initiated the protective response.

Electrical potentials were detected in the tentacles and lip, but not in the column (Fig. 2A). Potentials recorded from the tentacles were associated with tentacle contractions and therefore termed tentacle contraction potentials (TCPs). The term is only used here to identify the tissue from which the potentials were recorded and does not imply that the potentials recorded from scyphistomae are homologous with tentacle potentials observed in the hydrozoa (Passano and McCullough, 1962; Rushforth and Burke, 1971; Morin and Cooke, 1971; Ball, 1973).

Figure 2B shows a simultaneous recording of TCPs and tentacular movement. Characteristically, potentials occur 60 to 120 msec prior to the onset of tentacular contractions and are conducted along the length of the tentacle (Fig. 2C). A TCP has a conduction velocity of about 4 mm/sec, determined by the difference in arrival times between two suction electrodes placed along the length of a tentacle. Potentials in a tentacle were always independent of the electrical activity in other tentacles; therefore, there appears to be no conduction of TCPs between tentacles.

Potentials recorded from the lip were always associated with a localized retraction of the lip. Simultaneous recordings from two points in the lip indicate that potentials occur independently and correspond to movements only under the recording electrode; no conduction was found between the two recording points (Fig. 2D). Flaring did not occur when the suction electrodes were attached to the lip, so electrical potentials associated with flaring have not yet been recorded.

### *Strobila*

The onset of strobilation is indicated by an elongation of the polyp and the appearance of a groove marking the first ephyral primordium (Fig. 3). The polypoid tentacles still remain but are being absorbed. Marginal ganglia develop at the bases of the perradial and interradial tentacles and first appear as bulges at the bases of the tentacles. Adradial tentacles do not show these bulges and some have been eliminated in Figure 3 for clarity.

Electrical potentials recorded from the tentacles at this stage were always associated with tentacle contractions and appear to be the same as TCPs occurring in scyphistomae (Figure 3A). As with the scyphistoma, there was no conduction

# ELECTRICAL ACTIVITY IN THE POLYP

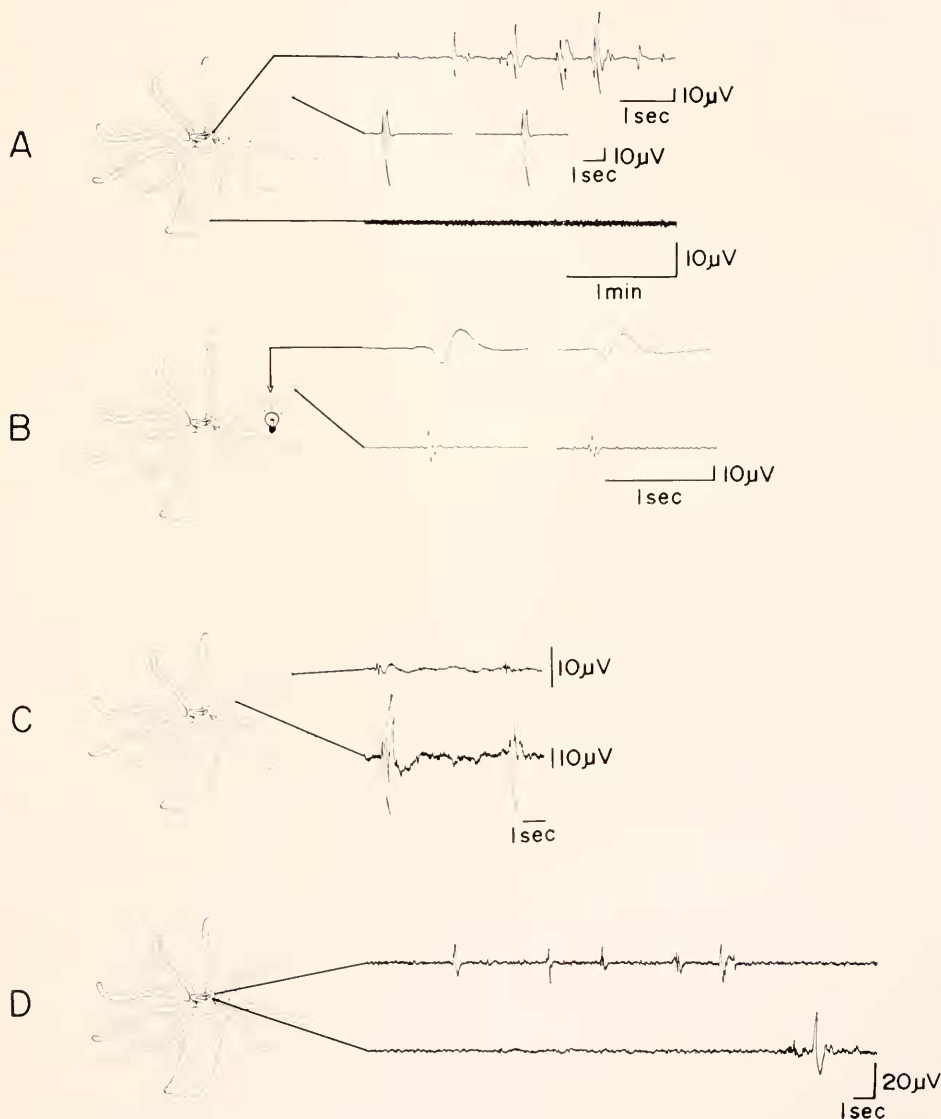


FIGURE 2. Spontaneous electrical activity in the scyphistoma. A, electrical recordings from the tentacles, lip, and column; B, electrical activity in a tentacle (lower record) and the associated movement recorded with the photoelectric-movement detector (upper record); C, conduction of the tentacle contraction potential (TCP); D, non-conduction of lip potentials.

## INITIATION OF STROBILATION

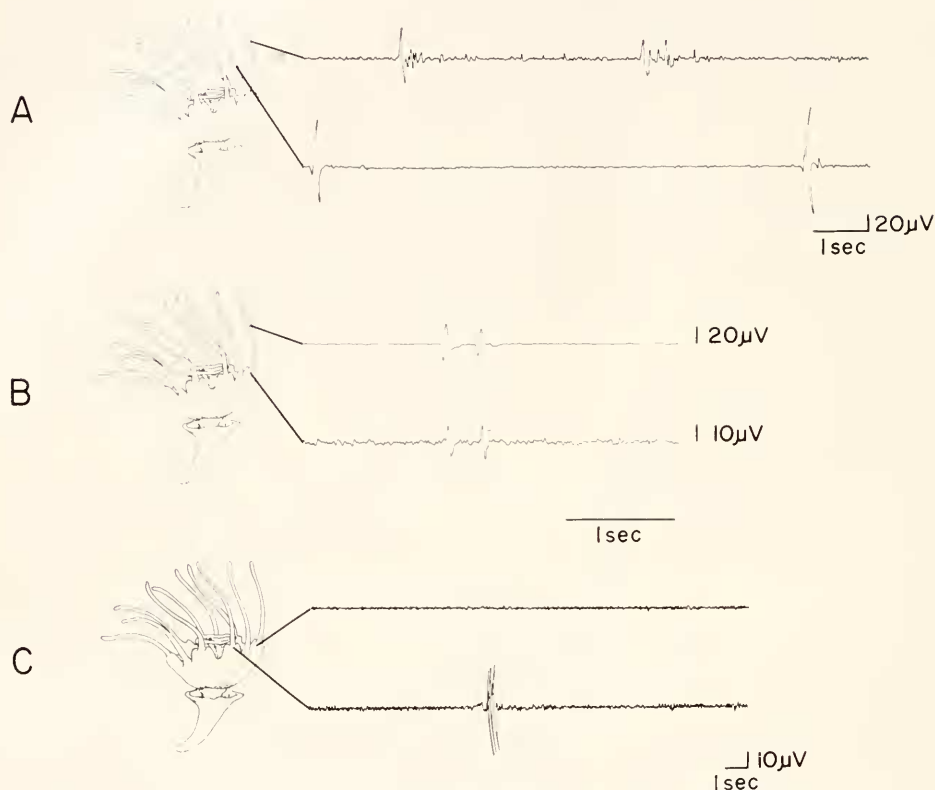


FIGURE 3. Electrical activity in an early strobila (no beating observed). A, TCPs recorded in two tentacles, one rhopalial and the other non-rhopalial; B, portions of records showing TCP conduction along a tentacle; C, electrical recordings between two rhopalial enlargements showing the absence of conduction in this early stage of strobilation.

between the tentacles (Fig. 3A). Each TCP was initiated distally and was conducted the length of the tentacle (Fig. 3B). Although marginal ganglion potentials are conducted to other marginal ganglia in the medusa (Passano, 1965), recordings from pairs of marginal ganglia primordia in the strobila demonstrate that TCPs were not conducted between them (Fig. 3C). After the tentacles have receded, TCPs also disappear and for a time the marginal ganglion primordia are electrically quiet.

As strobilation proceeds, the terminal ephyra begins to beat. Simultaneous recording of electrical potentials from a marginal ganglion and mechanical activity in the same arm demonstrated that the potentials corresponded one-to-one with beating movements of that arm and, therefore, are MGPs (Fig. 4A). However, at this early stage of strobilation the MGPs are not always conducted to the other



marginal ganglia (Fig. 4B). As development proceeds, a stage is reached where all MGPs are conducted to other ganglia as in the medusa (Fig. 4C). Once beating is established no particular pacemaker appears as the driving pacemaker. By

## BEATING

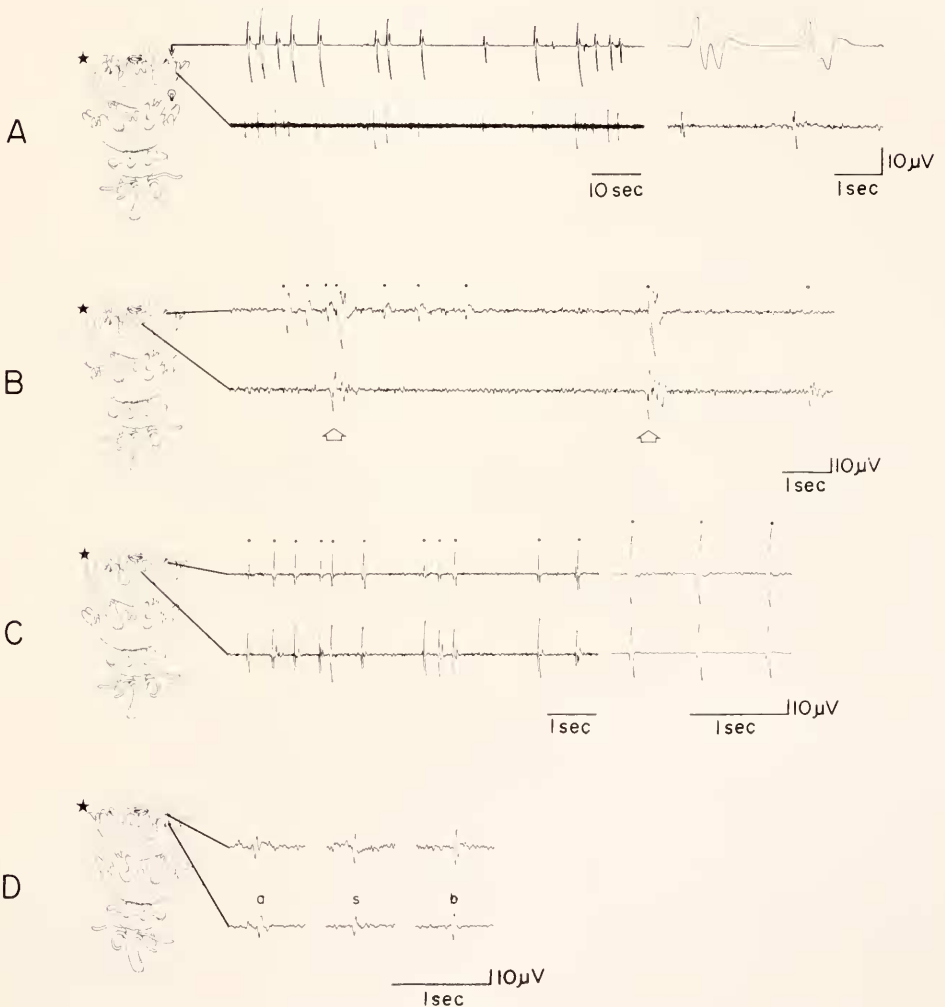


FIGURE 4. Electrical and mechanical activity in attached beating ephyrae. A, upper record, mechanical record of beating activity and in the lower record, the associated marginal ganglion potentials (MGPs); B, conducted (arrows) and nonconducted MGPs; C, conduction of MGPs fully established; D, shifting pacemaker dominance (see text for details). Dots indicate potentials associated with an observed beating contraction. The star indicates a beating ephyral bud.

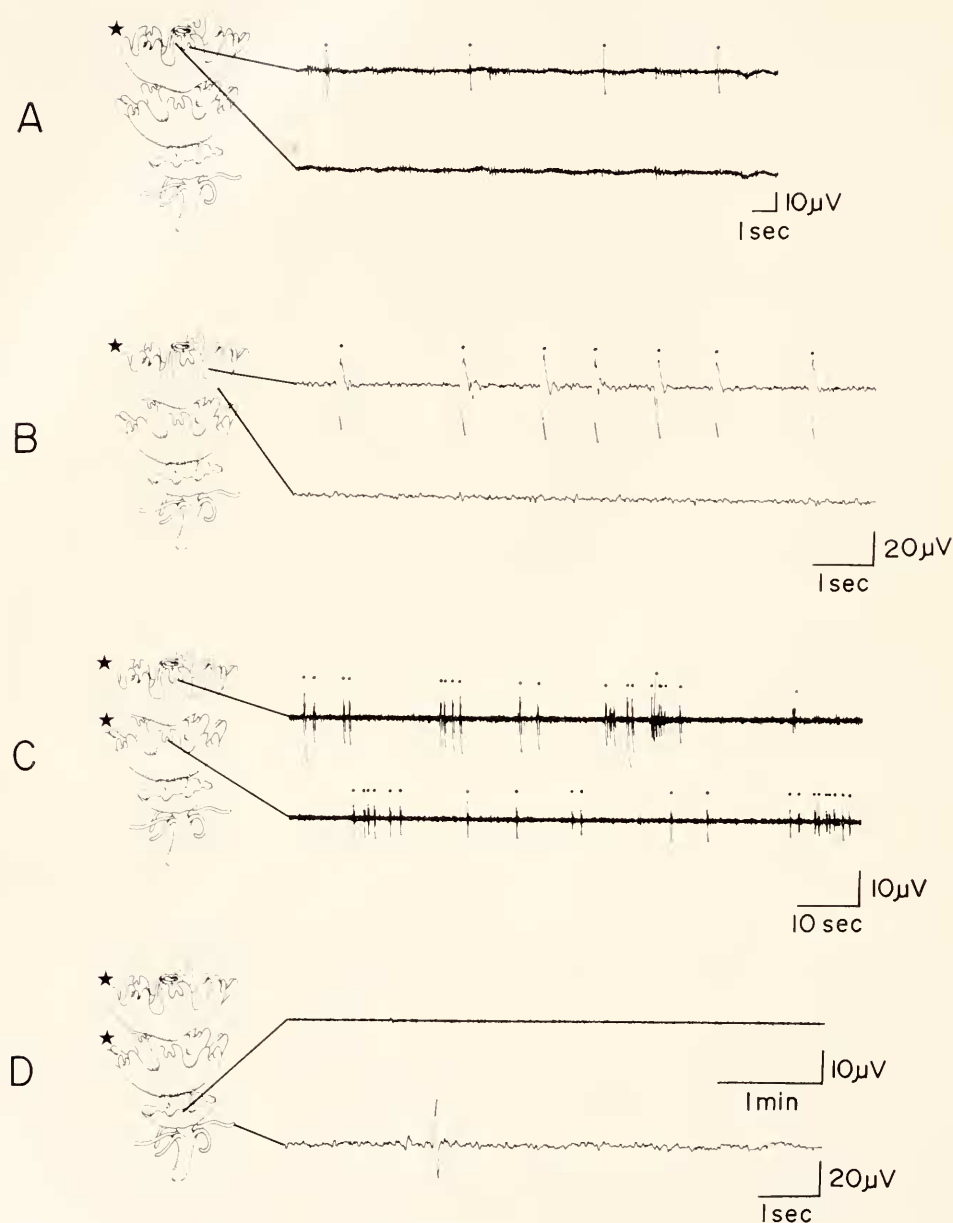


FIGURE 5. Electrical activity from different parts of the strobila. A, electrical records from a marginal ganglion (upper record) and from a lappet (lower record); B, upper record, electrical record from the subumbrella, and the lower record, from the exumbrella; C, marginal ganglion activity from two different attached and beating ephyrae indicating that MGPs are not conducted between ephyrae; D, electrical records from a nonbeating ephyra (upper record) and a tentacle from a resting polyp, the tentacle shows a TCP. Dots indicate potentials associated with observed beating contraction. The star indicates a beating ephyral bud.

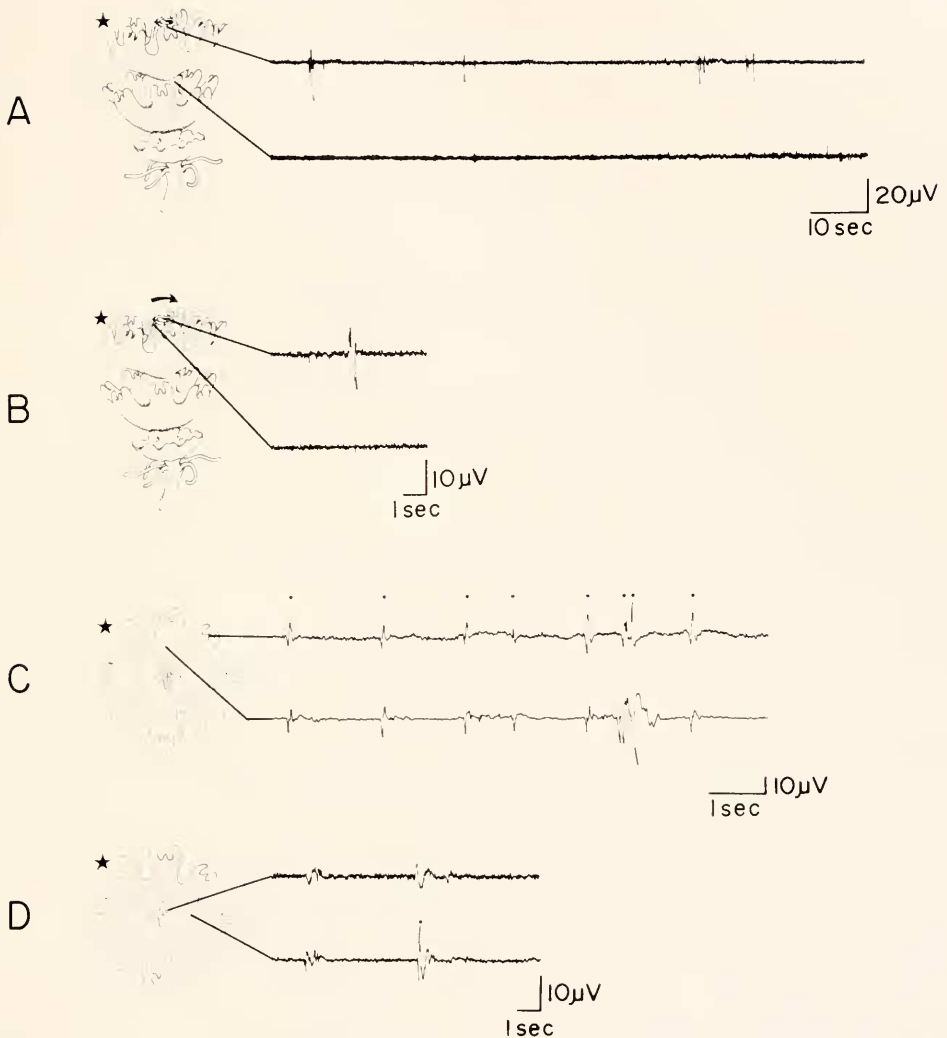


FIGURE 6. Electrical activity in a strobila. A, records from two manubria, the potentials are not conducted and were not associated with observed behavior; B, potentials recorded from two sides of a manubrium demonstrating the potentials associated with bending (arrow shows the direction of bending); C, top view of a strobila indicating the electrical activity from a marginal ganglion (upper record) and from a circular muscle in the area indicated; D, top view of a strobila showing the electrical activity in the manubrium and the circular muscles. Dots indicate potentials associated with an observed beating contraction. The star indicates a beating ephyral bud.

recording from two marginal ganglia separated by a third marginal ganglion, shifting pacemaker dominance is obvious. For example, three sets of potentials are shown in Fig. 4D: in the first set the lower MGP occurs after ("a") the upper MGP, in the second set both occur simultaneously ("s"), and in the third set the lower MGP occurs before ("b") the upper MGP.

## SPASM

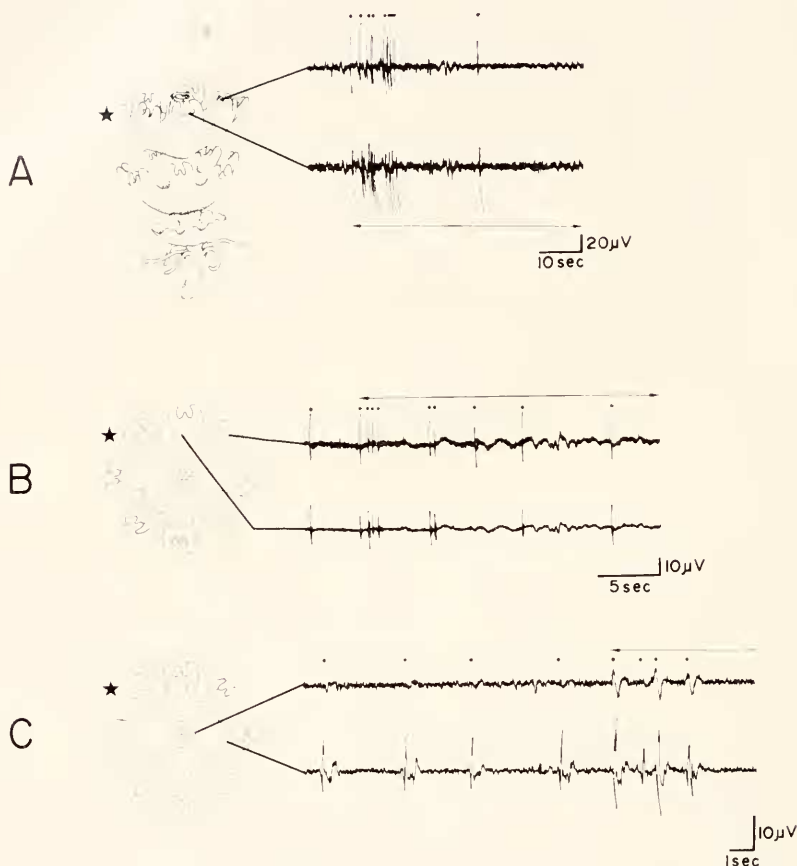


FIGURE 7. Electrical activity during spasm. A, recordings between two marginal ganglia showing the burst; B (top view of a strobila), electrical records between a marginal ganglion (upper record) and a radial muscle (lower record); C, (top view of a strobila) showing records of the electrical activity before a spasm from the manubrium (upper record) and from a radial muscle (lower record). The arrow indicates the duration of the spasm. Dots indicate potentials associated with an observed beating contraction. The star indicates a beating ephyral bud.

Following the appearance of conduction between marginal ganglia, conduction of MGPs could be detected in other parts of the beating ephyra. MGPs were never detected in the exumbrellar surface (Fig. 5A, B) but were routinely recorded from the subumbrellar surface in the areas of the radial and circular musculature (Fig. 5B, Fig. 6C, D). Occasionally, potentials which were associated with the beat occurred in the manubrium but this was unusual (Fig. 6D). MGPs from a

beating ephyral bud are not conducted downward to either nonbeating ephyrae or the resting polyp (Fig. 5D). Figure 5D also shows that nonbeating ephyrae do not produce MGPs, and the resting polyp produces only the typical TCPs. Electrical events between ephyrae on the same strobila were independent of each other (Fig. 5C).

Some potentials recorded from the manubrium were not associated with MGPs nor with any observable behavior. These potentials, to use Passano's (1965) terminology, are "cryptic" (Fig. 6A). In addition to MGPs and cryptic potentials, there is also electrical activity which corresponded with the bending of the manubrium (Fig. 6B). During the feeding response in a free ephyra, the manubrium bends toward an infolding arm (Horridge, 1956a). Potentials associated with this bending only occur on the contracting side (Fig. 6B).

Free ephyrae as well as ephyrae still attached to the strobila demonstrate spasm, a maintained oral flexion of the arms (Horridge, 1956a). Apparently, spasm is initiated by a burst of MGPs. Accompanying the burst a series of beats occur which draws all the arms inward (Fig. 7A). When the MGP burst is over, the arms remain folded, and further isolated MGPs occur (Fig. 7A), but during these isolated MGPs only the circular muscles contract. Gradually the radial muscles relax, and the arms are re-extended without any associated electrical activity. Figure 7B shows a complete electrical record of a spasm beginning with an MGP burst and continuing for a time with isolated MGPs. Also shown is the same MGP burst recorded from a radial muscle in another arm. A burst of electrical activity can also be recorded from the manubrium, which is associated with the MGP burst (Fig. 7C), but the isolated MGPs which occur after spasm is established are not reflected by any electrical activity in the manubrium. It should be noted that the experiments depicted in Figure 6D and Figure 7C are recordings from both DNN (in the manubrium) and GFNN (over the radial and circular muscles) in order to demonstrate coupling between the two nets (see Discussion for details).

Spasm in the strobila can be induced by electrical stimulation. Stimulation of the terminal ephyra resulted in spasm of the beating ephyrae in company with the symmetrical shortening of the whole column including the resting polyp. Stimulation of the resting polyp at the same intensity caused no response in the strobila. As stimulus intensity was increased, the excitation spread upwards causing spasm in the proximal, beating ephyra. Upon a further increase in stimulus intensity, spasm was initiated in the whole stack of beating ephyrae.

## DISCUSSION

Two types of behavior were observed in the polyp: first, local responses, restricted to one portion of the polyp and independent of activity in other parts of the animal; and, secondly, coordinated behavior involving integrated responses in several body parts. The presence of local responses suggests a single nerve net which is regionally differentiated so that isolated actions can be performed (Chapman, 1965). Previously, when two types of behavior have been observed in the same coelenterate tissue, two conduction pathways have been suggested and sometimes found histologically (Horridge, 1956a). Although double innervation from two nerve-nets cannot be excluded, a combination of epithelial conduction



in conjunction with a nerve-net is an equally sound hypothesis. The latter is supported by Chapman's (1965) histological observation of intermuscular junctions. The dimensions of these junctions were not discussed, but they may be low resistance pathways for epithelial conduction as found in many nerve-free coelenterate tissues (Mackie, 1970; Spencer, 1974b; Campbell, Josephson, Schwab, and Rushforth, 1976). Electrically excitable epithelia are relatively insensitive to  $Mg^{+2}$  anaesthesia and continue to respond to electrical stimulation after nervous conduction and muscle contractions have been abolished (Mackie and Passano, 1968). The epithelia of medusae or scyphistomae of *A. aurita* treated with excess  $Mg^{+2}$  are not electrically excitable; therefore, physiological evidence for epithelial conduction in *A. aurita* is lacking, and the duplicity of behavior in the tentacles remains unexplained.

The polyp does demonstrate two behaviors, feeding and the protective response, which are not regionally independent but involve coordination between body parts and, in the absence of demonstrated epithelial conduction, neuronal conduction is assumed. Feeding is a coordinated action between a tentacle and the mouth. Since the mouth gapes *before* the tentacle reaches the lip, mechanical coordination as suggested by Chapman (1965) is unlikely.

The coordinated feeding and protective response in the scyphistoma are similar to feeding and spasm in the ephyra. When an ephyral arm comes in contact with the prey, the arm moves independently toward the mouth as a radially segmented response. During spasm, the protective response of the ephyra, all the arms are coordinated and bend toward the mouth. Spasm, then, has been interpreted as the feeding response spread to the regionally segmented, independent, sensory nerve-net or diffuse nerve-net (DNN) by interneural facilitation (Horridge, 1956a). The similarity between the behaviors in the scyphistoma and the ephyra suggests that the protective response of the polyp is the feeding response spread to all the tentacles by interneural facilitation. If this assumption is correct, the ephyra retains two polypoid behaviors, feeding and the protective response. The coordination pathway for the protective response in the polyp apparently is in the oral disk since symmetrical column contraction can still take place when polyps are split from the pedal disk to just below the oral disk (Chapman, 1965). A bundle of neurites at the abaxial base of each tentacle has been identified (Chapman, 1965), but whether these bundles form a continuous ring which would provide a coordination pathway for the protective response is not known.

Tentacles and rhopalia (marginal ganglia) are considered to be homologous since rhopalia develop from tentacles and tentacles from rhopalia, as is demonstrated by intermediate teratogenic developmental forms (Thiel, 1966). In addition to the homology suggested by Thiel, certain functional analogies also exist between the tentacles and rhopalia. First, the tentacles seem to be the most sensitive structures of the polyp (Chapman, 1966) so also the rhopalia, since they have been shown to contain light sensitive areas (Horridge, 1959; Yamashita, 1957), respond to gravity (Horridge, 1959), and contain other sensory cells (Horridge, Chapman and MacKay, 1962; Russell, 1970; Chapman and James, 1973). Secondly, the rhopalia of the medusa and the tentacles of the scyphistoma are the most electrically active tissues in these animals. Finally, the electrical activity, the TCP, originates in the distal end of the tentacle and is conducted proximally similar to the conduction direction of the marginal ganglion potential (MGP) through

the giant fiber nerve-net (GFNN) to the swimming muscles in the medusa. This evidence indicates that the tentacles and rhopalia are functionally similar structures.

In the early stages of strobilation, when the strobila still possesses its original tentacles, the electrical activity is polypoid. It is interesting that although tentacles and marginal ganglia are probably homologous, there is not a smooth transition between TCPs and MGPs. During strobilation TCPs disappear with the resorption of the tentacles and the ephyral bud is, for a time, electrically quiescent until the occurrence of the first MGPs. In spite of the similarities between tentacles and marginal ganglia, pacemaker activity in the latter may develop *de novo*.

The first characteristic of the adult swimming system to be observed in a strobila was spontaneous beating of individual ephyral arms of the terminal ephyral bud. Potentials associated with the activity corresponded one-to-one with the mechanical activity in that arm. These potentials are MGPs, the same potentials used to drive the swimming muscles in medusae. At first the MGPs are not conducted to other marginal ganglia, but gradually the GFNN becomes functionally established, and the impulses conducted. When conduction is established the arms beat in unison.

In the ephyra, the DNN is distributed over the aboral surface, over the musculature and around the manubrium on the oral surface, while the GFNN is found only in the region of the marginal ganglia and over the radial and circular muscles (Horridge, 1956a). Therefore, the simultaneous recordings of electrical activity in the manubrium and radial musculature during spasm show that the DNN and GFNN become coupled during spasm. In fact, the DNN triggers the MGP burst which initiates spasm. In the medusa a single MGP can be triggered by a single or double DNN pulse after a delay, usually 1.55 sec in *Cassiopea* (Passano, 1973), but such a large delay was not observed in the ephyra. Pacemaker triggering systems are very common in hydrozoan polyps (Passano and McCullough, 1962; Josephson and Mackie, 1965; Morin and Cooke, 1971; Ball and Case, 1973). Furthermore, they are far more complicated than the MGP triggering system described here and are associated with non-nervous epithelial conduction.

The transition of a sessile, phlegmatic polyp to an active, swimming ephyral larva involves the development of a new nerve net, the GFNN, in addition to circular and radial striated muscles. The GFNN, with its pacemakers and through-conducting character, is used to initiate and coordinate swimming. The ephyra, however, does retain the polypoid nerve-net, the DNN, and two polypoid behaviors, feeding and the protective response (spasm) coordinated by the DNN. When ephyrae mature into medusae, the ephyral feeding and spasm responses are lost along with the radial musculature needed for these behaviors. Although feeding and spasm are lost in the medusa, the DNN remains, is sensory in function, controls marginal tentacle contractions, and serves to modulate pacemaker output (Romanes, 1877; Passano, 1965).

The comparison of the behavior and electrophysiology of the polyp, strobila, and medusa of *A. aurita* implies that as development proceeds, each subsequent stage acquires some new behavior while retaining some aspect from the previous stage. While the polypoid character of the DNN is not obvious in the medusa of *A. aurita*, it is clear in other adult scyphozoan medusae which retain the radial musculature. Adult individuals of *Cyanea capillata*, *Cassiopea andromeda* and

*Nausithöe punctata* all retain the radial muscles and utilize the DNN to control the asymmetrical compensatory movements used in the righting response (Horridge, 1956b). The compensatory movement in *C. capillata*, for example, occurs by the lengthening of the relaxation of the radial muscles by double innervation (Horridge, 1956b). This lengthening of relaxation is also observed during spasm and feeding in the ephyra of *A. aurita*. In *N. punctata*, feeding behavior is retained in the adult and closely resembles feeding behavior in the ephyra of *A. aurita*. Horridge (1956b) has found that the DNN in *N. punctata* resembles that of the ephyra of *A. aurita* histologically, physiologically, and anatomically. Horridge's observations on adult medusae with radial muscles provide additional evidence that the DNN in medusae is a polypoid structure; however, the behavior subserved by the DNN in the polyp is either lost or modified in the adult medusa. Behaviorally the ephyra is not a medusa. As the ephyra matures into an adult medusa, morphological and behavioral changes occur, not just growth.

#### SUMMARY

1. Electrical correlates of behavioral activity were observed in the lip and tentacles of the polyp, but none were detected during column contraction. The tentacles are the most electrically active tissue, and the potentials are conducted along the length of the tentacle, but conduction to other parts of the animal were not observed.

2. Although the tentacles of the polyp and the rhopalia of the medusa are probably homologous, the development of pacemaker activity during strobilation is not a smooth transition from tentacle contraction potentials (TCPs) to marginal ganglion potentials (MGPs). This result indicates that each pacemaker activity develops *de novo*.

3. Two types of behavior were observed in the polyp: local responses, and coordinated activity which involved integrated responses in several body parts. The coordinated responses indicate that neurological coordination can take place in the polyp. Furthermore, feeding and spasm in the ephyra are similar to feeding and the protective response in the polyp. This similarity suggests that both coordinated responses in the polyp are coordinated by interneural facilitation in the diffuse nerve net (DNN) as in the ephyra.

4. Swimming in the ephyra is a medusoid behavior but feeding and spasm are coordinated by the DNN and are polypoid responses. Therefore, the ephyra is a mixture of polypoid and medusoid behaviors. As the ephyra matures into an adult medusa both polypoid responses are lost, but the DNN remains to modulate pacemaker output and control marginal tentacle contractions. As development proceeds from polyp, to ephyra, to medusa, each subsequent stage acquires some new behavior while retaining some aspect from the previous stage.

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